Lesson: Anther
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Table of contents

Chapter: Anther

- **Introduction**
- **Structure**
- **Development of Anther and Pollen**
- **Anther wall**
  - **Epidermis**
  - **Endothecium**
  - **Middle layers**
  - **Tapetum**
    - **Amoeboid Tapetum**
    - **Secretory Tapetum**
    - **Orbicules**
    - **Functions of Orbicules**
    - **Tapetal Membrane**
    - **Functions of Tapetum**
- **Summary**
- **Practice Questions**
- **Glossary**
- **Suggested Reading**

Introduction

Stamens are the male reproductive organs of flowering plants. They consist of an anther, the site of pollen development and dispersal. The anther is borne on a stalk-like filament that transmits water and nutrients to the anther and also positions it to aid pollen dispersal. The anther dehisces at maturity in most of the angiosperms by a longitudinal slit, the stomium to release the pollen grains. The pollen grains represent the highly reduced male gametophytes of flowering plants that are formed within the sporophytic tissues of the anther. These microgametophytes or

1

pollen grains are the carriers of male gametes or sperm cells that play a central role in plant reproduction during the process of double fertilization.
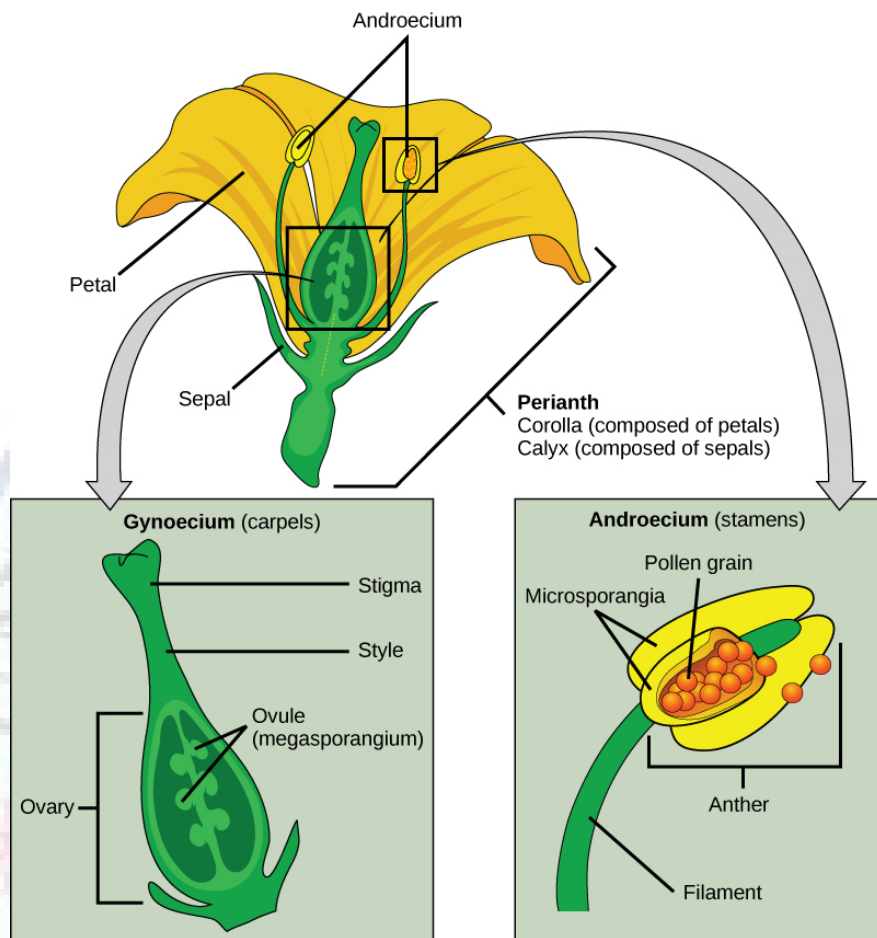

Figure 1. Diagram to show parts of a flower of an angiosperm
Source:
http://upload.wikimedia.org/wikipedia/commons/thumb/7/7f/Mature_flower_diagra
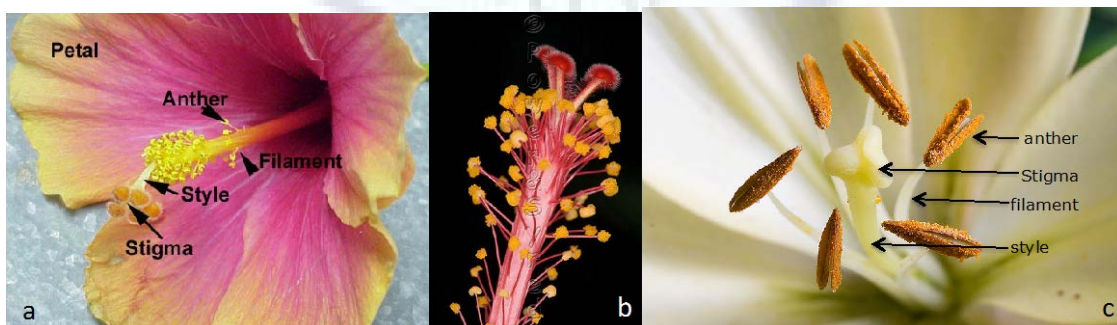m.svg/2000px-Mature_flower_diagram.svg.png

Figure 2

a. *Hibiscus* flower; b. *Hibiscus* stamens showing monothecous anthers; c. *Lilium* flower showing dithecous anthers

Source:

a. http://generalhorticulture.tamu.edu/h202/labs/lab2/flower-links/flower2.jpg
b. http://www.psmicrographs.co.uk/_assets/uploads/hibiscus-flower--hibiscus-sp---reproductive-organs-hib2-l.jpg
c. http://upload.wikimedia.org/wikipedia/commons/b/b4/Lilium_longiflorum_stamen.jpg

Structure

A typical anther is a bilobed, dithecous structure with two microsporangia in each lobe. Therefore, an anther is a tetrasporangiate structure with four microsporangia. The non-sporangial tissue that joins the two anther lobes is known as the connective. A single vascular strand is embedded in the connective. In each lobe the two microsporangia are separated by a strip of sterile tissue, the intersporangial septum. In a mature anther, the two sporangia in an anther lobe become confluent due to the enzymatic lysis of the septum to form a single locule or theca. In some plants such as *Hibiscus rosa-sinensis*, the anther is one lobed consisting of two microsporangia which are fused at maturity to form a single theca (monothecous).
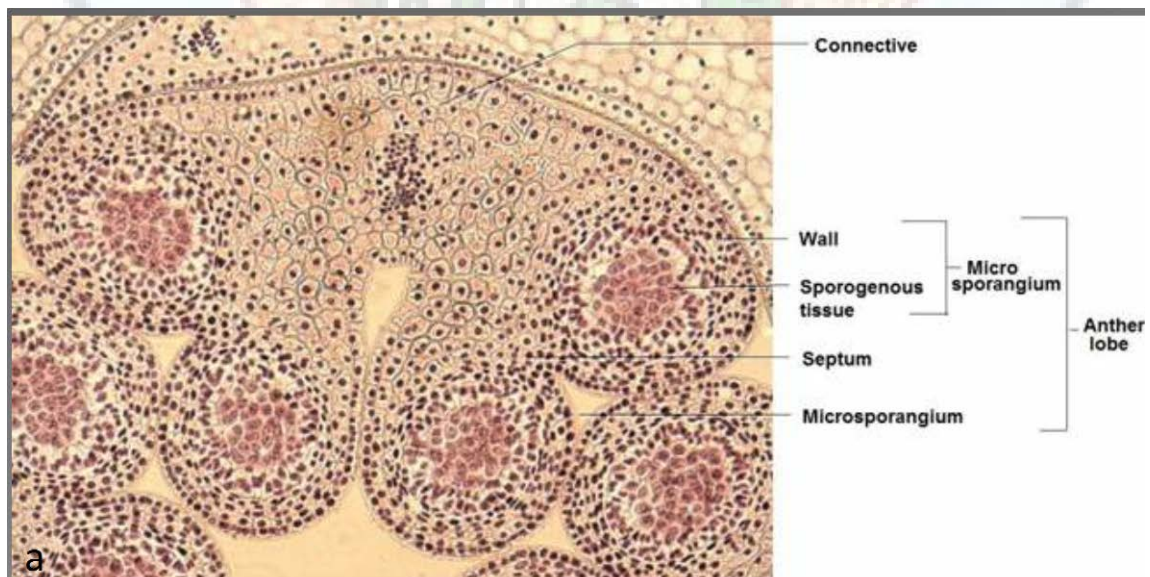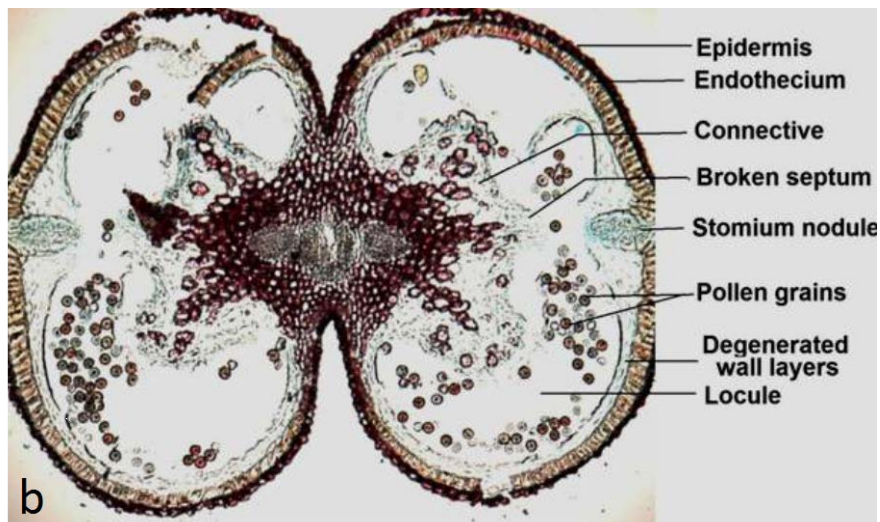
Figure 3. a. T.S. young tetrasporangiate anther at sporogenous cells stage showing the intact septum between the two microsporangia b. T.S. old dithecous anther prior to dehiscence showing the lysed septum and the merging of the two locules in an anther lobe.

Source (a and b) P. Chitralekha (2015) Laboratory manual 'Reproductive Biology of Angiosperms' Institute of Lifelong Leaning, UDSC, New Delhi (with permission)

Development of anther and pollen

A young undifferentiated anther comprises a homogeneous mass of cells bound by a well-defined epidermis. During its development a typical anther assumes a four-lobed appearance because of differentiation of four groups of archesporial cells in the hypodermal position corresponding to each microsporangium. These archesporial cells are distinct because of their large size, dense cytoplasm and conspicuous nuclei. Archesporial cells divide periclinally to form primary parietal cells towards the epidermis and primary sporogenous cells towards the interior of the anther. The cells of the parietal layer undergo a series of periclinal and anticlinal divisions to form the anther wall layers: an endothecium, usually 1-3 middle layers and a tapetum. The sporogenous cells function directly as the microsporocytes (the microspore mother cells / pollen mother cells/ meiocytes) or divide a few times to form secondary sporogenous cells before functioning as the microspore mother cells. The microspore mother cells become enclosed within a special callosic wall, undergo meiosis and give rise to tetrads of microspores. These microspores or pollen grains after their release from the callose wall, enlarge and undergo an asymmetric mitotic division to give rise to a large vegetative cell and a small generative cell. In many taxa, the pollen grains are shed at this stage (2-celled

4

pollen). In the others, the generative cell undergoes a second mitotic division and gives rise to two male gametes (sperm cells) before the pollen grains are shed from the anther (3-celled pollen). Two-celled pollen grains undergo the second mitotic division in the pollen tube after pollen germination.
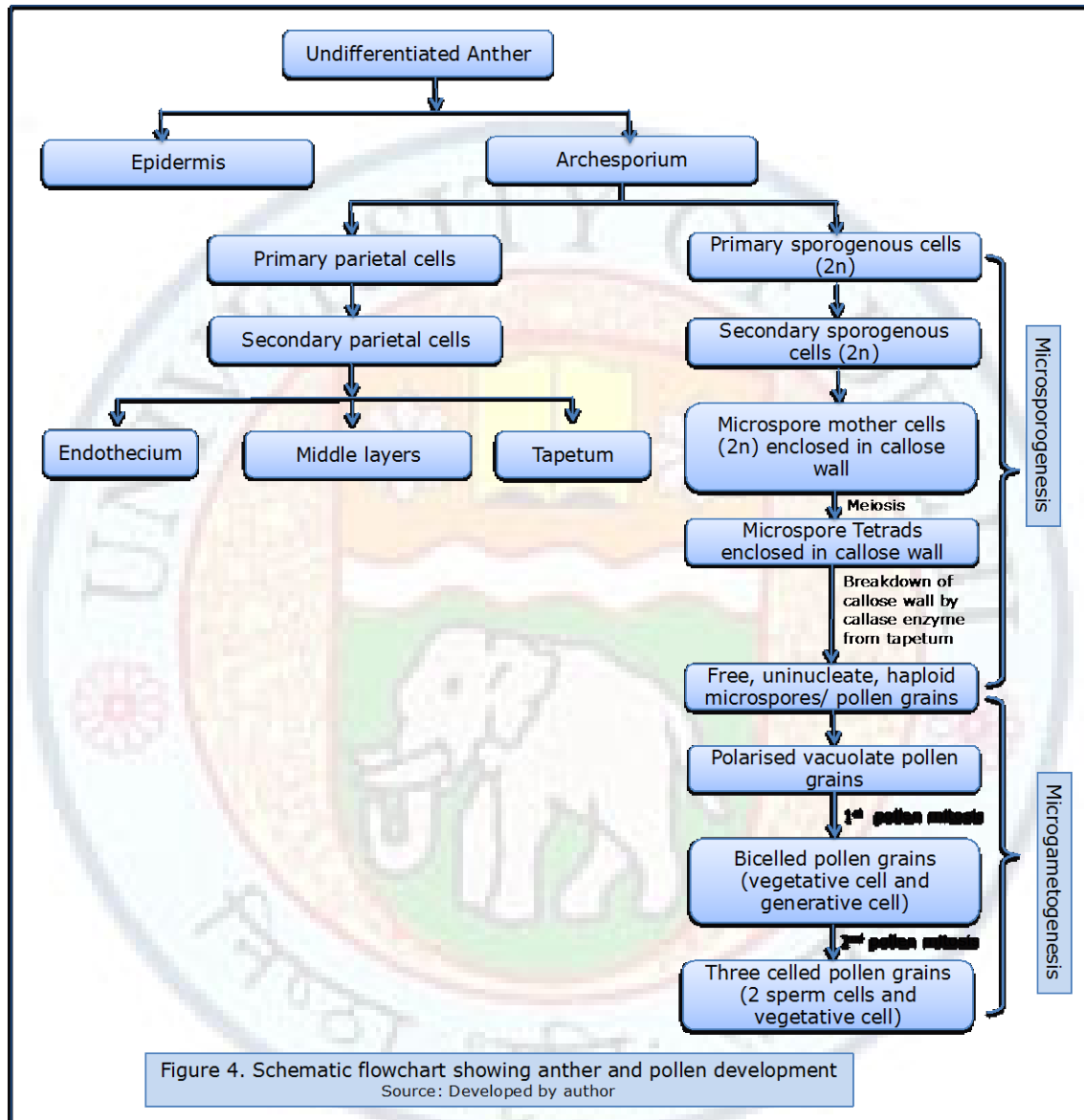
Figure 4. Schematic flowchart showing anther and pollen development
Source: Developed by author

Microsporogenesis

The series of events that lead to the development of haploid uninucleate microspores within the microsporangia is known as microsporogenesis.

Microgametogenesis

The events that include the development of the microspores into the microgametophytes/ pollen grains containing the sperm cells are called as microgametogenesis.
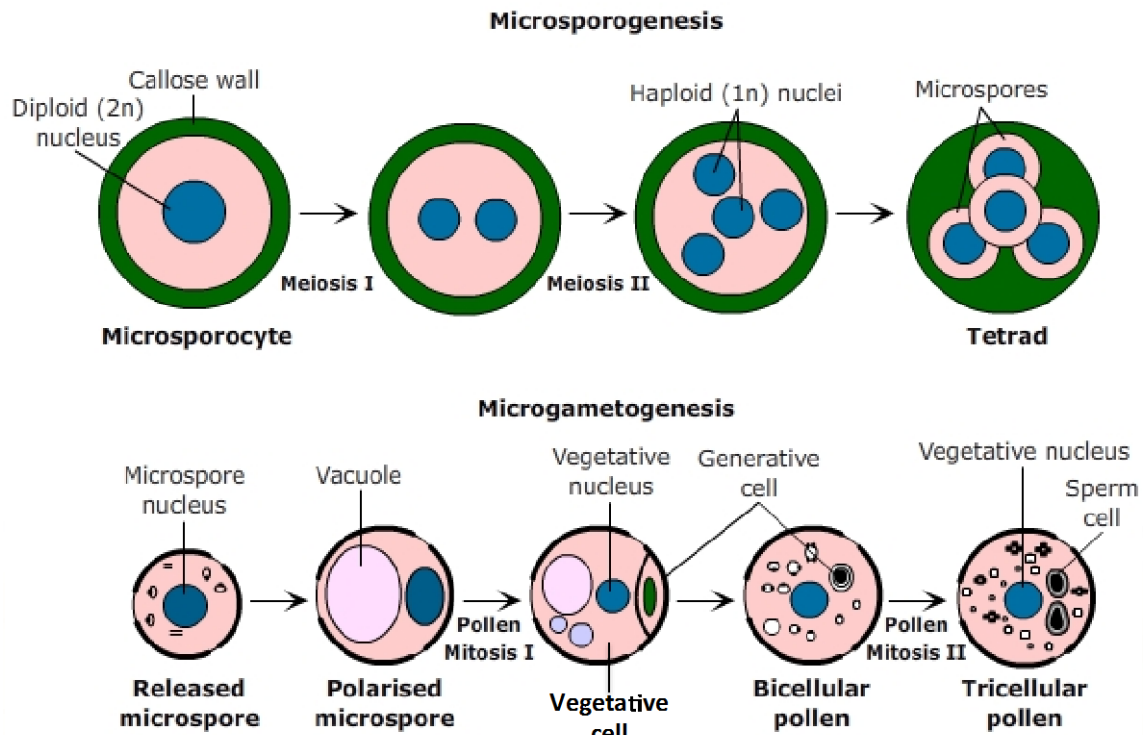

Figure 5. Diagrammatic representation of the sequence of events in microsporogenesis and microgametogenesis.
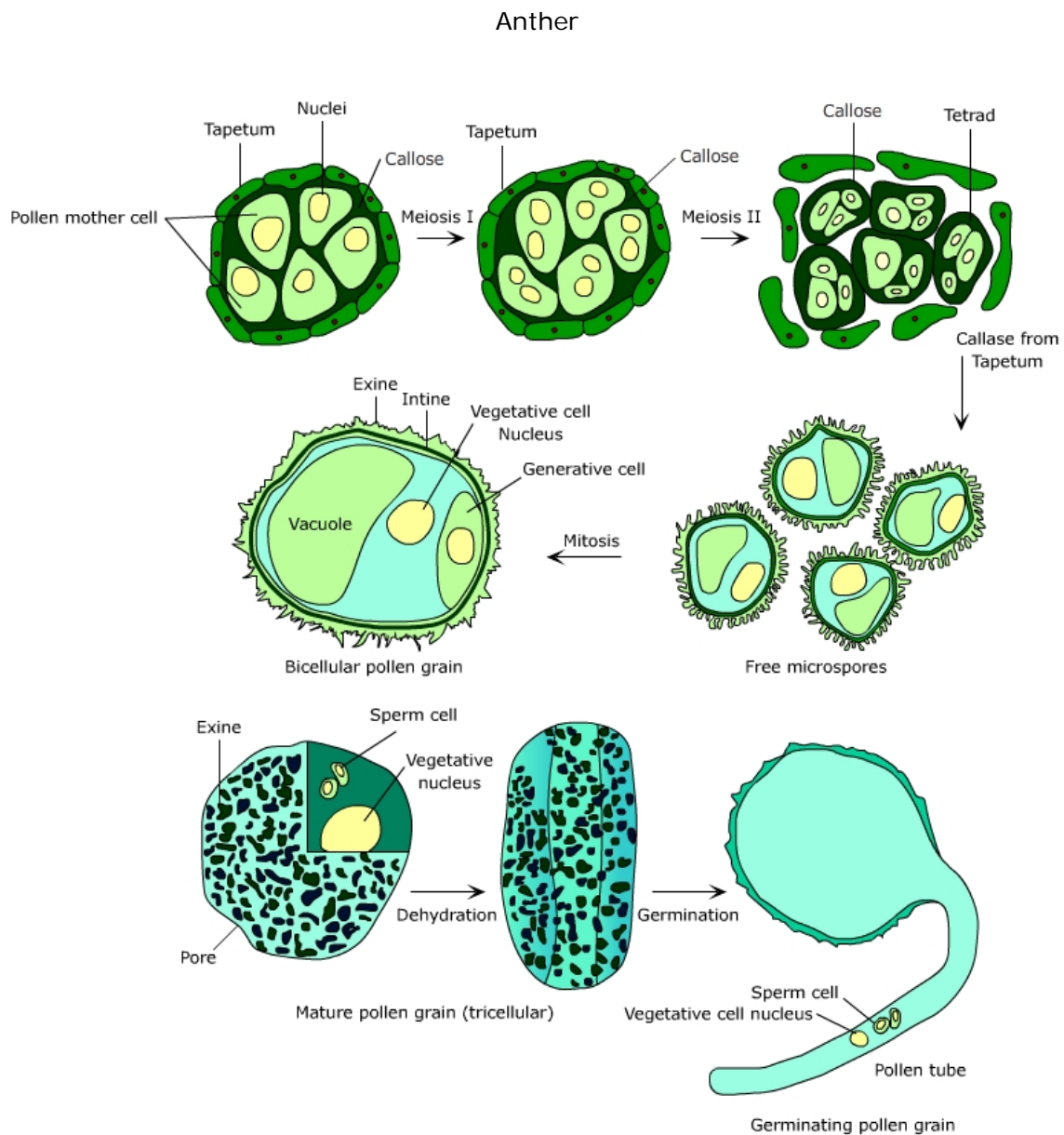Source: Author, ILLL Inhouse

Figure 6. Schematic Diagram showing pollen development.
Source: Author, ILLL Inhouse

Anther wall

The well-differentiated anther wall comprises

- Epidermis
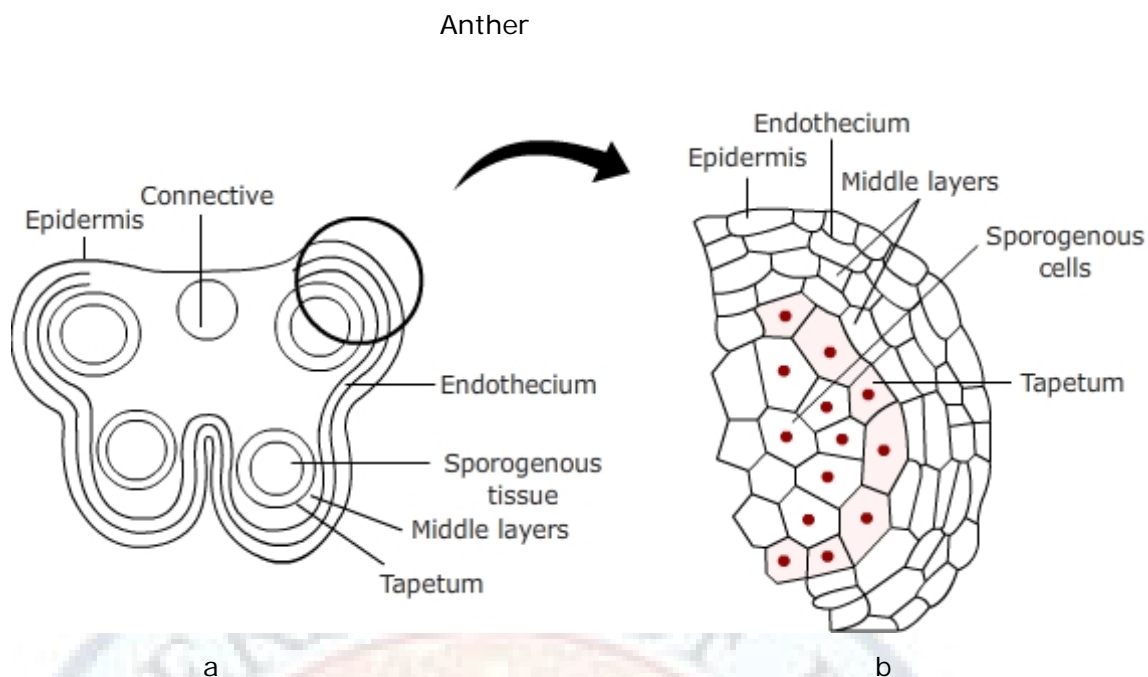- Endothecium
- Middle layers
- Tapetum

Figure 7 a and b. Diagrammatic view of TS anther showing wall layers

Source: Author, ILLL Inhouse

Epidermis

The epidermis is the outermost layer of the anther and has a protective function. The epidermis prevents water loss from the anther, together with the endothecium provides structural support to the anther and plays a role in the anther dehiscence (Goldberg et al. 1993). In a mature anther, the epidermal cells are greatly stretched and flattened. The epidermal cells in the presumptive stomium region differentiate into small, specialized cells that split at anther maturity to facilitate dehiscence and release of pollen grains.
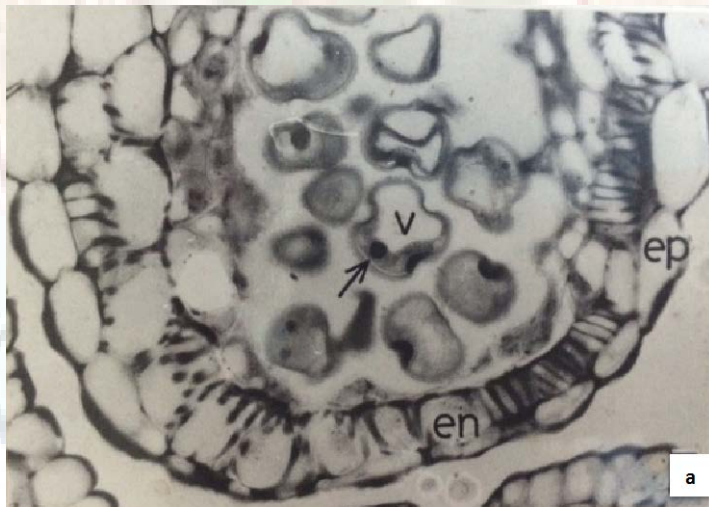
Endothecium

The endothecium is the hypodermal layer of the anther wall (present beneath the epidermis) and persists in the mature anther. It is usually single layered and is present only in the protuberant part of the anther in majority of angiosperms. The cells of the endothecium are generally uninucleate and highly vacuolated. A few starch grains are often found in the cells. These cells become radially elongated and attain maximum development when the anther is ready to dehisce for the discharge of pollen. The endothecium cells are characterized by deposition of fibrous bands of lignocellulosic secondary thickenings that arise from the inner tangential walls and run outward and upward. The outer tangential walls remain thin. The endothecial cells around the junction of the two sporangia do not undergo secondary thickening.

These fibrous bands are essential for providing the mechanical force for anther dehiscence.

> **Endothecium and Anther Dehiscence**
>
> During anther and pollen development, the tangential swelling of the epidermis and endothecium increases the circumference of the locule wall, but the inner locule wall dimensions remain fixed because of the endothecium thickenings. This outer enlargement combined with the inner fixed dimensions causes the locule wall to bend inwards resulting in disruption of stomium cells. Water evaporation from the exposed anther at the time of anthesis causes the dehydration and shrinkage of the endothecium and epidermal cells. The localized thickenings of the endothecium resist this shrinkage and cause the locule to bend outwards (Wilson et al.2011). The outward stress thus created pulls apart the stomium cells resulting in dehiscence of anther.
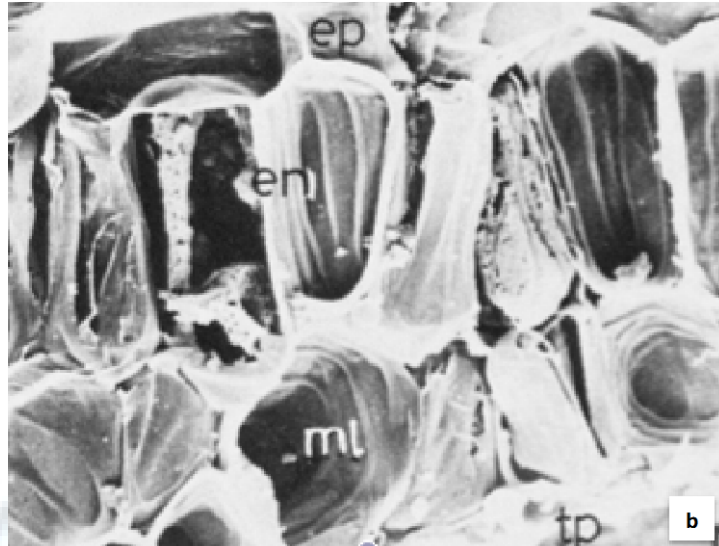
Figure 8.

    a. *Prosopis juliflora* anther locule at vacuolate pollen grain stage showing distinct secondary thickenings in the endothecial cells.

    b. *Simmondsia chinensis* SEM anther wall showing epidermis, endothecium with fibrous bands and a single middle layer (v. vacuole; en. Endothecium; ep epidermis; ml. middle layer; tp. tapetum)

Source: Author

Middle layers

In, general there are 1-3 middle layers; more layers are found in anthers of some angiosperms such as *Lilium* while in others, such as *Wolffia* and *Vallisneria*, middle layers are absent. The cells are flattened, thin-walled, uninucleated and vacuolated. They are rich in reserve food material such as starch, which gets mobilized during the development of pollen. Middle layers are generally transient or ephemeral and become crushed during meiosis in the microspore mother cells. In plants like *Lilium* and *Ranunculus,* one or more middle layers may persist until the dehiscence of anthers (Bhojwani et al. 2014). In some plants, the middle layers may develop secondary thickenings similar to the endothecium cells as in *Heliconia* species (Simao et al 2007) and assist in dehiscence of anther.

Tapetum

Tapetum is the innermost layer of the anther wall and completely surrounds the sporogenous tissue. It is usually single layered and has several nutritive and

10

secretory functions related to pollen development, pollination and pollen germination. The tapetum in many angiosperms is of dual origin. The outer portion of the tapetum is contributed by the parietal layer while the inner portion is derived from the connective tissue. The tapetum cells contain prominent nuclei and dense cytoplasm with an abundance of organelles such as mitochondria, plastids, endoplasmic reticulum, dictyosomes, vesicles and ribosomes. The cells often become polyploid through mitotic divisions of nuclei (multinucleate), formation of restitution nuclei, endomitosis or polyteny, indicating a high metabolic activity. The tapetum attains its maximum development at the tetrad stage of microsporogenesis. During microgametogenesis it starts degenerating and is completely degenerated by the time the anther is ready to dehisce.

There are two basic types of tapetum:

> Amoeboid or invasive or periplasmodial or syncytial tapetum
> Secretory or glandular or parietal or non-syncytial tapetum

Amoeboid/ Invasive Tapetum

Amoeboid tapetum is common in the monocots e.g. *Arum italicum*, *Tradescantia bracteata*, *Butomus umbellatus, Typha spp.* However, Poaceae members (grasses) are an exception, which usually show secretory tapetum. Amoeboid tapetum is also present in most members of the dicot family Asteraceae eg. *Helianthus annuus, Ambrosia trifida.*

Amoeboid/ invasive type of tapetum is characterized by:

❖ An early breakdown of the inner tangential and radial walls of its cells (usually during meiotic prophase or until the tetrad stage),
❖ Invasion of tapetal protoplasts into the anther locule,
❖ Fusion of tapetal protoplasts to form a multinucleate tapetal periplasmodium/syncytium that closely engulfs/invests the developing microspores. Ultrastructural studies of the plasmodial tapetum indicate that the tapetal periplasmodium is an organized and functional unit with normal organelles and high metabolic activity.

❖ The tapetal protoplasts remain in close contact with the developing pollen making the passage of nutrients more efficient than that in the secretory tapetum. Species with amoeboid tapetum characteristically do not produce orbicules (also called as ubisch bodies). However, sporopollenin-like granules on the tapetal remnants in species with amoeboid tapetum have been reported, that are generally smaller in size than the orbicules produced by secretory tapetum. Eg. *Tradescantia virginiana* (Tiwari and Gunning 1986),

11

Butomus umbellatus (Fernando and Cass 1994) and *Persea palustris* (Furness and Rudall 2001).
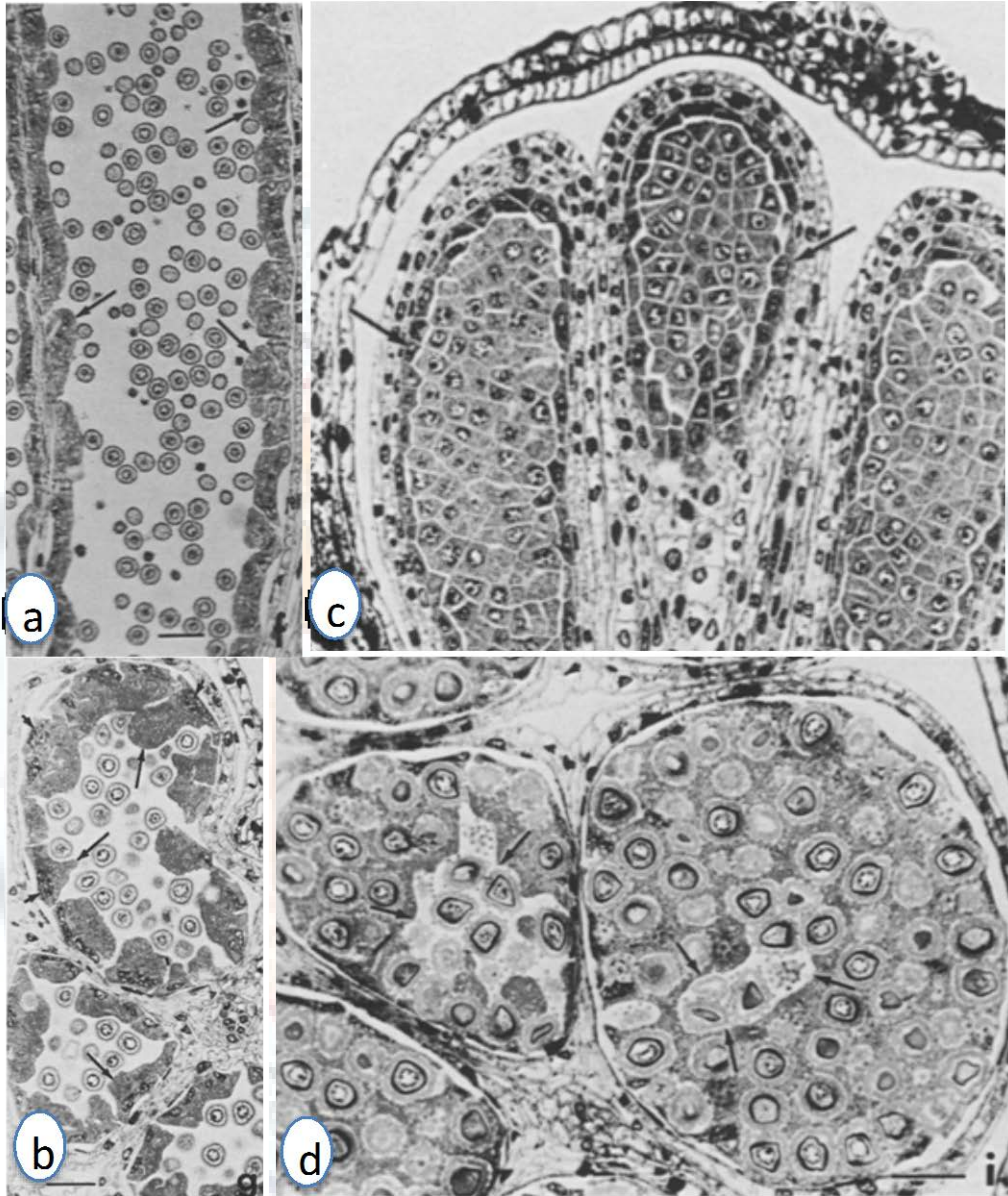

Figure 9. Invasive tapetum stages in *Ambrosia trifida*; bars: 20 µm. a. Longisection of locule with young microspores recently released from tetrads; tapetum shows first signs of swelling (arrows). b. Cross section of three locules showing tapetal cells that are more swollen and beginning to invade locule with microspores (arrows). Note tapetal nuclei against locule periphery (arrowheads), also in c. c. Slightly later stage in cross section; tapetal protrusions (arrows) engulfing microspores. d. Locules in cross section at later microspore stage; merged tapetal cells have invaded most, but not all (arrows at boundary) of each locule.

Source: Adapted from Lersten and Curtis, Invasive tapetum and tricelled pollen in *Ambrosia trifida* (Asteraceae, tribe Heliantheae 1989 Plant systematics and Evolution volume 169 pages 237-243
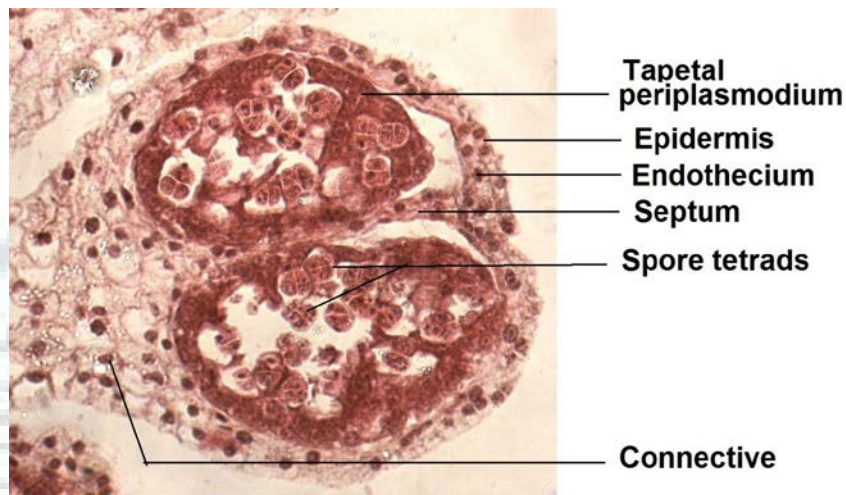
Figure 10. *Tradescantia* TS anther showing tapetal periplasmodium around the spore tetrads
 Source: P. Chitralekha (2015) Laboratory manual 'Reproductive Biology of Angiosperms' Institute of Lifelong Leaning, UDSC, New Delhi (with permission)

Secretory/ Parietal Tapetum

Secretory tapetum is common in dicots (*Citrus limon*, *Capsicum annuum*, *Helleborus foetidus*, *Prosopis juliflora*, *Lycopersicon peruvianum*). However, it is present in some families of monocots like Poaceae (*Sorghum bicolor*, *Avena sativa)* and Liliaceae (*Lilium longiflorum)*. In secretory tapetum, the tapetal cells remain in their original position and maintain their identity throughout microspore development. The cells eventually undergo degeneration in situ towards the end of pollen development. Transport of substances from the tapetal cells into the locule may occur through exocytosis or through secretion across the plasma membrane. A characteristic feature of the secretory tapetum is the presence of sporopollenin granules/bodies termed orbicules or ubisch bodies. The progenitors of orbicules are called as pro-orbicules or pro-ubisch bodies, which after accretion of sporopollenin

form the orbicules or ubisch bodies. The pro-orbicules in many plants originate from the endoplasmic reticulum of secretory tapetal cells (Echlin and Godwin, 1968; Vijayaraghavan and Chaudhry, 1993; Garcia et al. 2002; Rosenfeldt and Galati 2005). The orbicules are known to transport sporopollenin between the tapetum and the developing pollen exine.
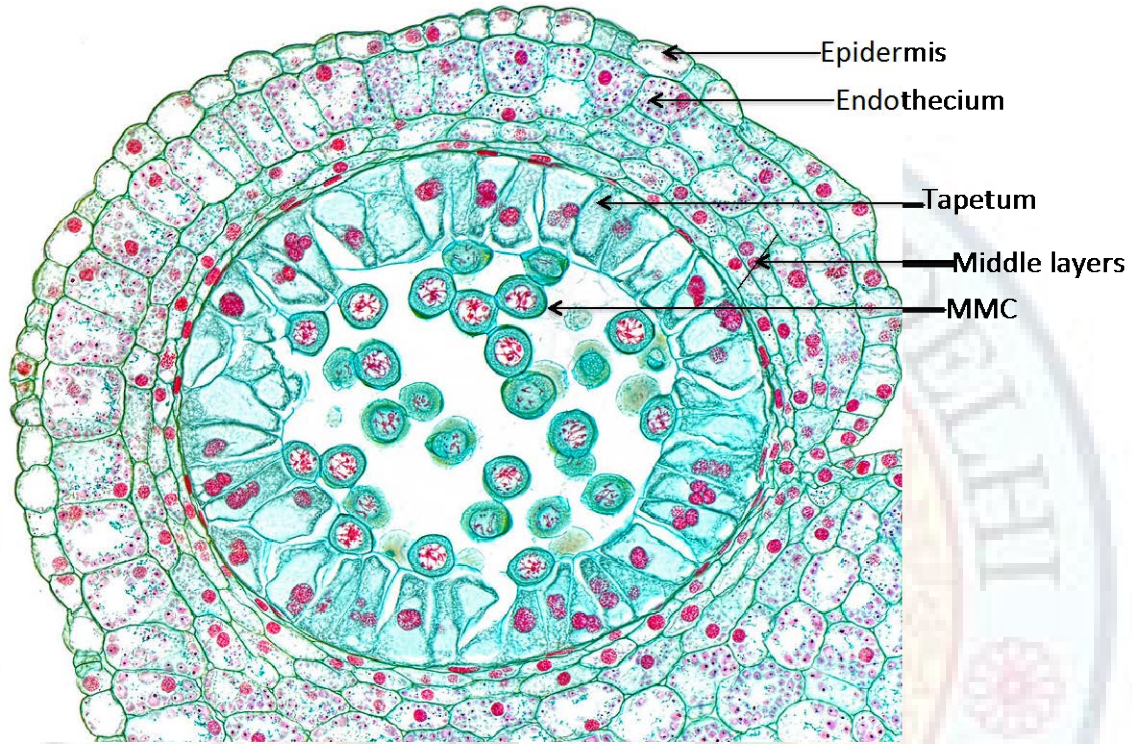

Figure 11. TS microsporangium *Lilium* showing secretory tapetum and microspore mother cells (mmc) undergoing meiosis (seek permission)
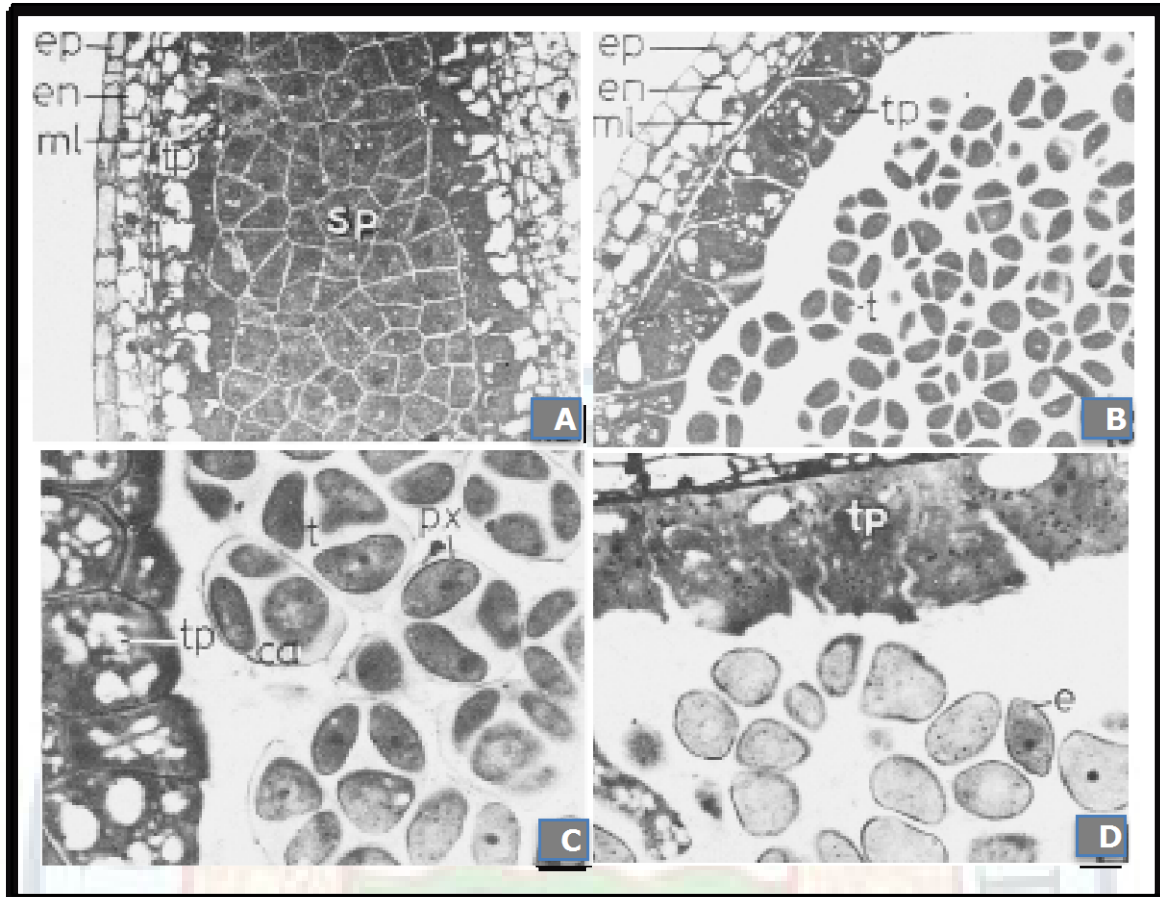Source: http://images.fineartamerica.com/images-medium-large-5/lilium-ts-anther-m-i-walker.jpg

14

Figure 12. *Simmondsia chinensis*

A. Longisection of young anther showing the secretory tapetum and the central mass of sporogenous cells.

B and **C**. Anther locules to show the secretory tapetum at microspore tetrad stage. The tapetal cells are large, densely stained, remain in situ and show secretory activity. The tetrads are enclosed in a thick callose wall

D. The tapetal cells surround the microspores just released from the tetrads. The callose wall around them is dissolved. A thin exine is visible around each microspore.

(**ca**, callose, **e**, exine, **en**, endothecium, **ep**, epidermis, **ml**, middle layer, **px**, primexine, **sp**, sporogenous cell, **t**, tetrad, **tp**, tapetum)

Source: Adapted from Chaudhry and Vijayaraghavan, 1995 Proceedings of Indian National Science Academy B61, no.3 pg 199-208

Intermediate types of tapetum

An intermediate, invasive non-syncytial type of tapetum is reported in plants like *Canna* (Tiwari and Gunning, 1986) and *Heliconia* (Simao et al. 2007) where the tapetal cell walls break down and the tapetal protoplasts invade the anther locule but do not fuse to form a periplasmodium. Secretory tapetum is believed to be the most primitive type from which other types have been derived, showing a tendency towards more efficient nutrition.

Orbicules

Orbicules are small sporopollenin particles usually smaller than 1 µm to a few micrometers in diameter but frequently fuse into larger compound aggregates. They originate as lipid droplets in the tapetal cytoplasm (as pro-orbicules or pro-ubisch bodies) and are extruded into the anther loculus where they rapidly acquire sporopollenin coating to form the orbicules or ubisch bodies. They are usually seen lining the inner tangential walls of the secretory tapetum in close contact with the pollen grains. The orbicules develop simultaneously with the growing pollen exine and are composed of sporopollenin similar to the pollen exine. In angiosperms, the ornamentation of the pollen exine and that of the orbicule wall often show a striking parallelism. The sporopollenin condenses both upon the pro-orbicular cores and the exine initials to form the orbicules and the species-specific mature exine of pollen grains. Pollen grains with echinate exine often show spiny orbicules.
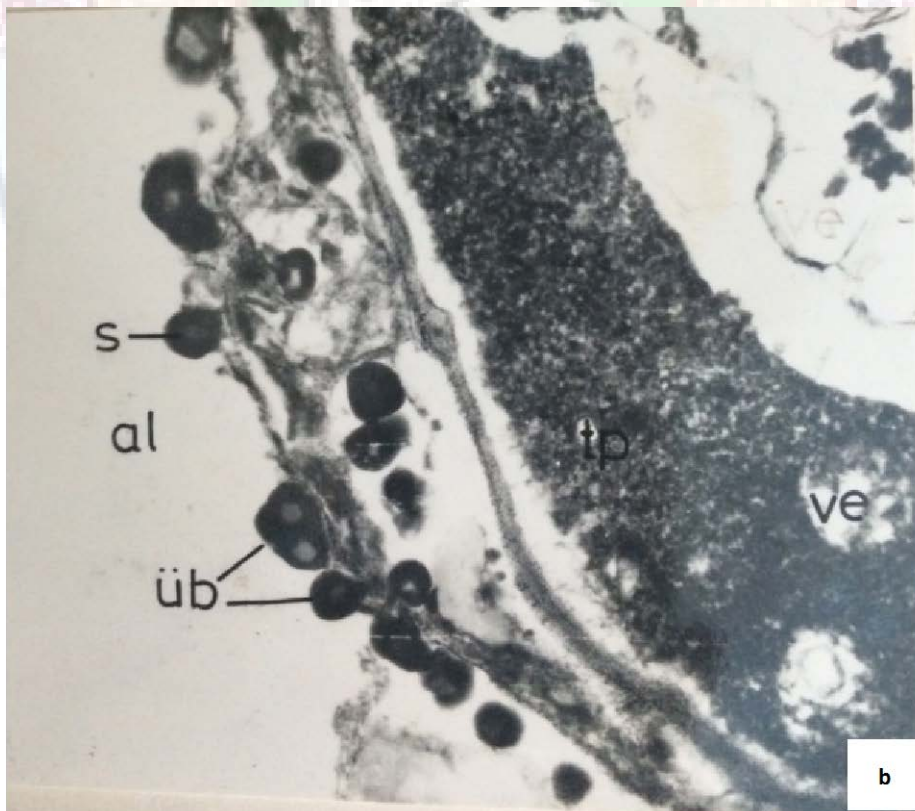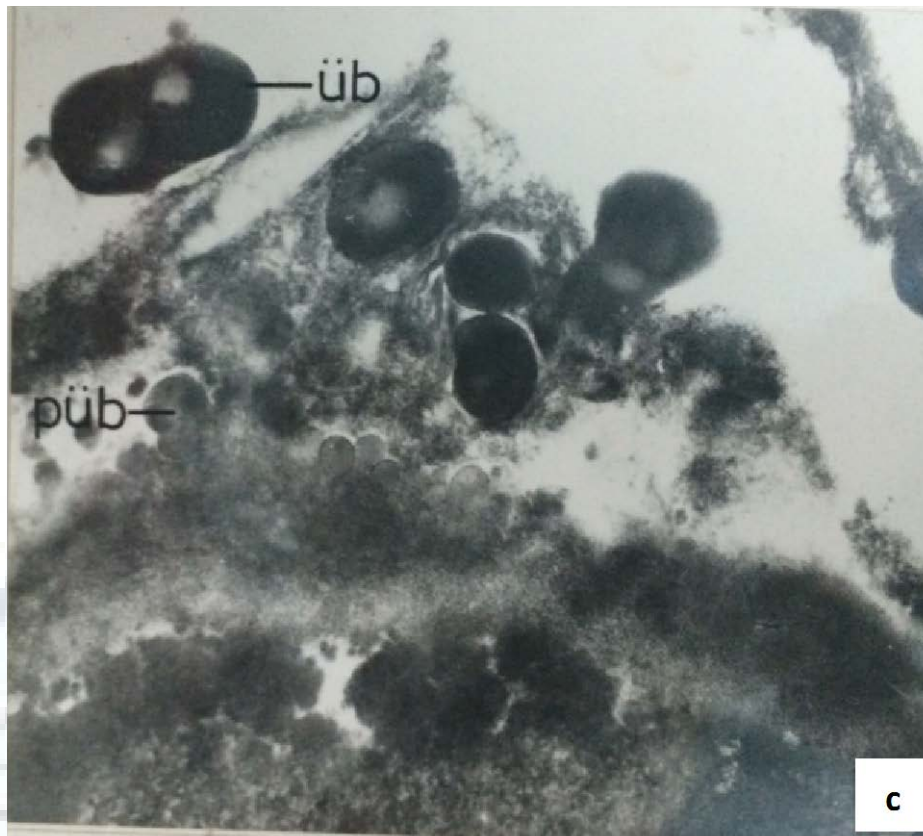
Figure 13 a-c *Prosopis juliflora*

a. TEM Anther locule showing secretory tapetum and ubisch bodies coated with sporopollenin. The tapetal cytoplasm is dense and rich in secretory vesicles. The ubisch bodies are distinct near the tetrad enclosed in callose wall (only one microspore visible).

b. and c. TEM ubisch bodies at uninucleate stage of microspores. Each ubisch body shows a globular lipid core (pro-ubisch body) with a homogenous sporopollenin coat around it. A few ubisch bodies have fused to form compound ubisch bodies. Note the extrusion of pro-ubisch bodies from the tapetal cytoplasm in c. (al, anther locule; ml, middle layer; pub, pro-ubisch body, s, sporopollenin; tp, tapetum; ub, ubisch body; ve, vesicle)

Source: Author

A survey on orbicule distribution throughout angiosperms has revealed that the orbicules are found all over of flowering plants with an evolutionary trend towards orbicule absence in more derived clades (Verstraete et al. 2014). It also demonstrates that the correlation of orbicule presence with non- amoeboid tapetum types holds true and that the presence of orbicules is a convenient proxy for tapetum characterization.

Functions of Orbicules

- The orbicules have been implicated as a transport mechanism of sporopollenin for the external thickening of the exine, the pattern of which is laid in the tetrad stage by the spore cytoplasm.
- Orbicules are considered by many as just by-products of the tapetum metabolism with no specific function.
- They have been implicated as vectors of allergens in the tapetum of some plants and may be important in pollinosis, which is a serious allergenic reaction in the lower part of the lungs (Vinckier and Smets, 2005).
- Orbicular wall may play an active role in pollen dispersal by forming a hydrophobic locule surface from which pollen can easily detach.
- Since ornamentation of pollen exine offers useful characters for systematics, orbicules with a similar ornamentation might also have taxonomic value.

Tapetal membrane

The development of the tapetum is associated with the formation of an acetolysis resistant membrane, the tapetal membrane. The tapetal membrane originates from the secretions of the tapetal cells and is largely made up of sporopollenin, insoluble polysaccharides such as cellulose and small amounts of pectin and callose (Shivanna 2003). In species characterized by secretory tapetum, the tapetal membrane is formed on the inner surface of tapetal cells (towards the locule). On this membrane are studded the orbicules or ubisch granules. In species characterized by a plasmodial tapetum, the membrane is formed on the outer surface of the tapetum (towards the endothecium). According to Heslop-Harrison, this extra tapetal membrane probably acts as culture sac enclosing the developing microspores together with the labile periplasmodium.

Functions of Tapetum

The tapetum is functionally one of the most important wall layers of the anther and pollen sterility is invariably associated with tapetal abnormality.

- The tapetum is involved in the supply of nutrients to the developing pollen (nurse tissue). As the tapetum encloses the sporogenous tissues all around, any nutrients entering the sporogenous cells have to pass through the tapetum. In the plasmodial tapetum, the tapetal protoplasts are in close association with the developing pollen facilitating the transport of nutrients.

19

In secretory tapetum, the nutrients are released into the locule fluid through exocytosis or secretion, from where they are taken up by developing pollen.

- The tapetum plays a role in the breakdown of callose wall around the microspore tetrads by secreting an enzyme callase (β-1,3 glucanase). Tapetal activation of callase enzyme at the right stage is very important for normal development of pollen. Precocious release of callase by tapetum is responsible for cytoplasmic male sterility in *Petunia*.

- The tapetum supplies sporopollenin precursors to the pollen exine. The precursors are secreted by both plasmodial as well as the secretory tapetum that are synthesized into sporopollenin, the chief component of the exine of the pollen wall. In many taxa, the blueprint of the exine is laid down while the tetrads are still enclosed in callose walls, but the bulk of the exine is deposited by the sporopollenin synthesized by the tapetum after the release of microspores from the tetrads. Orbicules formation in the secretory tapetum is also associated with sporopollenin synthesized by the tapetum.

- The tapetum supplies pollen coat substances called as pollenkitt and tryphine. Following tapetum degeneration, these are deposited on and within the pollen exine. Tryphine and pollenkitt help in the adherence of the pollen grains in clusters and to the insect pollinators to aid pollination. They also seal the pollen grains at the apertures to reduce the water loss. Tryphine is a complex mixture of hydrophilic and hydrophobic substances while pollenkitt is largely made of hydrophobic lipids containing species-specific carotenoids, glycolipids and glycoproteins. Pollenkitt (pollen glue in German) forms an oily viscous coating around the pollen grains of many angiosperms pollinated by insects whereas tryphine seems to be restricted only to the family Brassicaceae (Pacini and Hesse, 2005). The stickiness, odour and yellow/ orange colour of the pollen grains is because of the pollenkitt. The biological functions of the pollenkitt have been implicated in pollen dispersal, as an insect attractant, protecting the pollen against the damaging effect of ultraviolet radiation and as the pollen borne substance involved in sporophytic incompatibility.

- The tapetum is involved in the supply of pollen wall proteins. The pollen wall contains proteins derived from the pollen cytoplasm (intine proteins) as well as the proteins derived from the tapetum (exine proteins). The exine proteins of the tapetal origin are present in the inter-bacular cavities of the exine. The interaction of these recognition proteins in the exine with the recognition proteins produced by the stigma plays an important role in

20

sporophytic self incompatibility by which the stigma either rejects incompatible pollen or accepts and stimulates the germination of compatible pollen. If pollen lands on an incompatible stigma, these proteins induce the formation of callose-plugs in the stigma as well as pollen grains and block the growth of pollen tube.
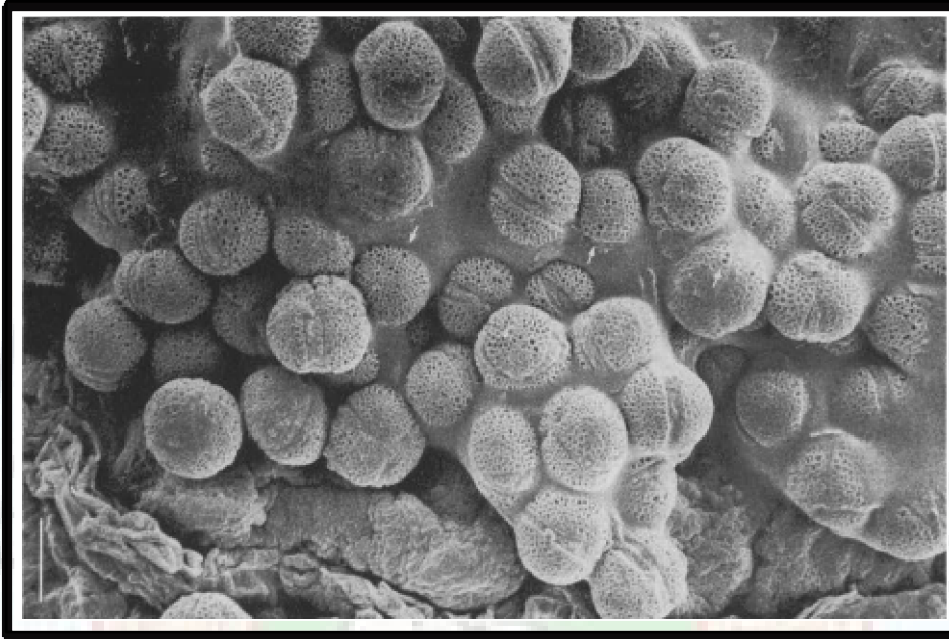

Figure 14. Pollen grains of *Hamamelis mollis* glued together with pollenkitt
Source: Michael Hesse (1980) On the Attachment of Pollen on Flower-Visiting Insects by Pollenkitt and Viscin Threads Plant Systematics and Evolution 133, 135 - 148

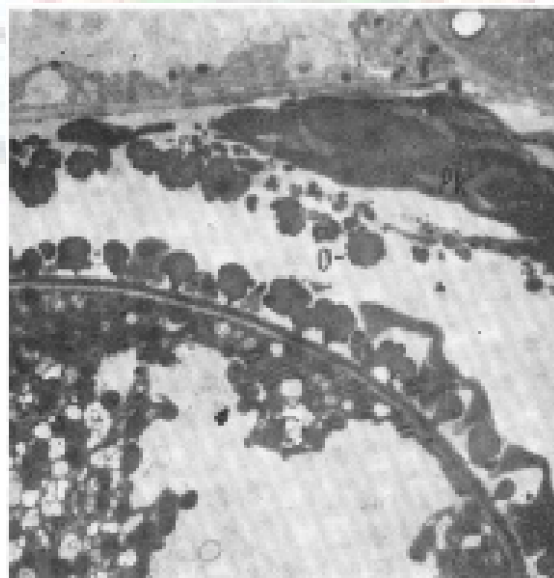Institute of Lifelong Learning, University of Delhi

Figure 15. TEM anther *Lilium* locule showing pollenkitt on the surface of pollen grain and near the anther wall. (O, orbicule; pk, pollenkitt)

Source: Reznickova and Willemse (1981) The function of the tapetal tissue during microsporogenesis in *Lilium* Acta Societatis Botanicorum poloniae Vol. 50, nr 1-2: 83-87

Summary

➢ An anther is the site of pollen development and dispersal. The microgametophytes or pollen grains develop within the anther and carry the sperm cells to the female reproductive structures for double fertilization.

➢ A typical anther is a tetrasporangiate, bilobed structure with two microsporangia in each lobe. The two sporangia in each lobe become confluent at maturity due to the lysis of the septum.

➢ The events that lead to the development of microspores or pollen grains within the microsporangia are called microsporogenesis. The development of the microspores into the microgametophytes or pollen grains containing the sperm cells is called as microgametogenesis.

➢ The well-differentiated anther wall comprises an epidermis, an endothecium, 1-3 middle layers and the tapetum.

➢ The epidermis is protective, provides structural support, prevents anther water loss and the specialized epidermal cells in the stomium region split at maturity to facilitate anther dehiscence and release of pollen.

➢ The endothecium develops fibrous bands of lignocellulosic secondary thickening that provides the mechanical force for anther dehiscence.

➢ The middle layers are short-lived and get crushed during pollen development. The cells store nutrients for the developing pollen.

➢ Tapetum plays a crucial role in pollen development. There are two basic types of tapetum: amoeboid/ invasive/ syncytial/ periplasmodial tapetum and secretory/glandular/ non-syncytial/ parietal tapetum. Orbicules or Ubisch bodies are a characteristic feature of secretory tapetum.

➢ The tapetum is involved in the supply of nutrients to the developing pollen, supply of sporopollenin precursors to the pollen wall exine, release of pollen coat substances (pollenkitt and tryphine), supply of pollen wall proteins and release of callase enzyme for the breakdown of callose wall around the microspore tetrads.

Glossary

Amoeboid tapetum: A type of tapetum in which the walls of the tapetum cells degenerate prior to fusion of the protoplasts into a plasmodium that invades the anther locule and ensures close contact with the developing microspores. This type of tapetum is characterized by the absence of orbicules in most plants.

Anther: An anther is the part of a stamen that produces and releases the pollen grains.

Callose: Callose is a plant polysaccharide, composed of glucose residues linked together through β-1,3 linkages and is also called β-glucan. It is thought to be manufactured at the cell wall by callose synthases and is degraded by β-1,3-glucanases. It is laid down at the plasmodesmata of plant cell walls, at the site of wounds to block pest and microbial attack, at the cell plate during cytokinesis, during pollen development around the pollen mother cells, around the megaspore mother cell in ovules and also in the germinating pollen tubes.

Anther dehiscence: Splitting of the anther at maturity along a built-in line of weakness.

Anther locule: A liquid filled cavity within the anthers in which the pollen grains develop and ripen.

Endothecium: The hypodermal layer of the anther wall characterized by the deposition of fibrous bands of lignocellulosic thickenings that provides the mechanical force for anther dehiscence.

Microgametogenesis: The process of formation of male/micro-gametes from the microspores.

Microsporogenesis: The series of events that lead to the development of haploid, uninucleate microspores within the microsporangium.

Orbicules or Ubisch bodies: Small sporopollenin bodies characteristically present in the secretory tapetum and may function in transport of sporopollenin to the exine.

Pollenkitt: An oily, thick, viscous coating present over the pollen grain surface of many insect pollinated species that helps in adhering pollen grains together, adhering of pollen to insect pollinators and also to the stigma surface.

Secretory tapetum: A type of tapetum where the tapetal cells maintain their identity and position throughout microspore development and degenerate in situ towards the end of pollen development. This type of tapetum is characterized by the presence of orbicules.

Tapetum: The innermost layer of the anther wall that plays an important secretory and transport function in pollen development, pollination and pollen germination.

Practice Questions

Q.1 Explain the structure of a typical tetrasporangiate anther with well differentiated wall layers.

Q.2. Differentiate between the process of microsporogenesis and microgametogenesis.

Q.3. Differentiate between amoeboid and secretory tapetum.

Q.4. Write a short note on the orbicules and the tapetal membrane.

Q.5. What is pollenkitt? What is its biological significance?

Q.6. Enumerate the various functions of the anther tapetum.

Q.7. Fill in the blanks

i. Pro-ubisch bodies are a characteristic feature of …………… tapetum.

ii. The thick viscous oily coating present on surface of pollen of entomophilous plants is called as ……………………

iii. The generative cell of the pollen divides mitotically to give rise to two…………. cells.

iv. The sequence of events that lead to the development of haploid microspores within the microsporangia is called as ……………………

v. The layer of the anther wall, which plays a role in dehiscence of anther, is called………………

vi. The tapetum associated with the formation of a periplasmodium is called as …………………..

Suggested readings

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